

Mature and developing kelp bed community composition in a glacial estuary

Sarah Beth Traiger*, Brenda Konar

University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK 99775, United States

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ABSTRACT

The assembly and maintenance of biological communities is influenced by environmental factors, which are predicted to shift with climate change. Glaciers are melting at increasing rates, delivering sediment and fresh water to coastal habitats. We hypothesized that environmental factors related to glacial discharge would be correlated to the initial recruitment and colonization of sessile communities in kelp beds, and to the abundance of mobile epibenthic invertebrates and adult kelp. To test these hypotheses, cleared rocks were placed at six sites at 10-m depth across a gradient of glacial-influence in Kachemak Bay, Alaska and the percent cover of the initial recruitment and the subsequent progression of the sessile community was monitored over 18 months. Small mobile invertebrates (such as limpets and chitons) were also monitored on these rocks for 18 months. Lastly, larger invertebrates (such as sea stars) and adult kelp were surveyed over the same time period along transects in the immediate vicinity of the cleared rocks. Environmental factors (sedimentation rates, salinity, temperature, irradiance, and nutrient concentration) were concurrently monitored at each site. Recruitment and subsequent colonization varied along the glacial gradient. At sites with higher sedimentation rates, recruitment and the subsequent developing community was dominated by barnacles with little or no kelp recruits and other macroalgae and high temporal variation in availability of bare space. At more oceanic sites, these communities were characterized by a slow increase in cover of encrusting and upright macroalgae, also with high variability among sites. Mobile invertebrates and adult kelp were more abundant at oceanic sites than the glacial sites. Using distance-based linear models, inorganic sedimentation rate was correlated to patterns of kelp bed recruitment and colonization and to the abundance of mobile invertebrates and adult kelps in the surrounding area. Changes in inorganic sedimentation with climate change may alter how kelp beds are distributed and structured in glacial estuaries.

1. Introduction

Kelp beds are important ecosystems around the world. Kelp beds support a wide range of commercial, recreational and subsistence fish and invertebrate species (Efird and Konar, 2014; Hamilton and Konar, 2007; Markel and Shurin, 2015). The primary productivity in kelp beds is large, and as such, kelp beds feed nearshore and offshore communities via detritus and through kelp drift (Abdullah et al., 2017; Duggins et al., 2016; Yorke et al., 2013). Kelp is harvested for subsistence and commercial use, as well as for herring roe, which use kelp blades for substrate (Holen et al., 2012; van Tamelen and Woodby, 2001; Vásquez et al., 2012). Hence kelp beds are important to nearshore and offshore ecosystems and to human communities.

Kelp beds naturally experience environmental and biological disturbances that result in space being cleared for recruitment. Recruitment can be affected by larval or propagule supply, environmental conditions, and biotic interactions. Hydrodynamic factors such

as upwelling variability and current direction can affect propagule supply and the pool of species that can recruit to an area (Billot et al., 2003; Menge, 2000). Environmental conditions such as high sedimentation may also prevent certain organisms from establishing (Balata et al., 2007). Kelp microscopic stage growth, survival, and subsequent recruitment may be inhibited by high temperature, low nutrient conditions (Ladah and Zertuche-Gonzalez, 2007; Mabin et al., 2013; Nielsen et al., 2014) and interactions between temperature and salinity (Fredersdorf et al., 2009). The effects of eutrophication and disturbance on kelp recruitment can vary by species, resulting in compositional changes to kelp beds (Carnell and Keough, 2014). The study of initial recruitment and early colonization can give clues to ecological processes such as propagule supply, competition, and disturbance (Benes and Carpenter, 2015; Gagnon et al., 2005; Konar and Iken, 2005; Maggi et al., 2012). Recruitment is critical for sustaining populations, so understanding the effects of multiple stressors on recruitment is needed to assess population and community stability (Perkol-Finkel and Airoidi,

* Corresponding author.

E-mail addresses: sbtraiger@alaska.edu (S.B. Traiger), bhkonar@alaska.edu (B. Konar).

2010).

Contrasts between communities in recently disturbed patches and more established communities can indicate environmental factors that affect adult populations. The community that persists to reproduce may be very different than the community that initially recruits. Localized mortality of macroalgae and invertebrates sometimes follows influxes of sediment or fresh water (Branch et al., 1990; Karsten, 2007). Kelp responses to warming can vary among co-existing species, potentially leading to changes in kelp bed species composition with future temperature increases (Hargrave et al., 2017). Kelp beds may be replaced by filamentous turf communities under persistent high sedimentation rates and elevated temperature (Bogen, 2009). Sea star movement and feeding can be inhibited by low salinity conditions (Agüera et al., 2015; Held and Harley, 2009). Variation in epibenthic invertebrate assemblages has been attributed to organic sedimentation, sediment type, and wave exposure (Eddy and Roman, 2016). Persistent changes in environmental conditions, such as increasing temperature at an ocean warming hotspot, can result in large scale changes in kelp biomass and species composition of kelp communities (Filbee-Dexter et al., 2016).

Glaciers are important features in high latitudes with direct connections to the nearshore environment (tidewater glaciers) or indirect connections through rivers fed by glaciers. Glaciers are melting at accelerating rates (Neal et al., 2010), resulting in increased glacial discharge that reduce water temperatures and salinities, increase sedimentation rates, reduce light availability (Wiencke et al., 2007), and degrade substrate quality (Spurkland and Iken, 2011). These environmental changes have been observed to diminish benthic biodiversity and macroalgal abundance (Spurkland and Iken, 2011; Włodarsk-Kowalczyk and Weslawski, 2001); however, it is not yet understood whether these declines are due to differences in survival of initial recruits or drivers impacting subsequent colonization. This study investigated the role of environmental factors in a glacial estuary in structuring several components of kelp bed communities including 1) the recruitment and subsequent colonization of the sessile community on bare rocks over a time period of 18 months, and 2) mobile epibenthic invertebrate and adult kelp abundance. Identifying potential drivers of kelp beds among the environmental factors affected by glacial melt will aid in selecting variables for further study. This study also contributes to the discussion of how environmental drivers structure kelp bed communities in glacial estuaries.

2. Material and methods

2.1. Study site

Kachemak Bay, Alaska, is a high latitude estuary whose kelp beds are exposed to an environmental gradient influenced by glaciers. It is divided into an inner and outer bay at the Homer spit, which extends several kilometers into the bay (Fig. 1). Oceanic water from the Alaska Coastal Current enters the outer bay along the southern shore and flows counter-clockwise to then exit along the northern shore (Schoch and Chenelot, 2004). The outer, southern bay is free of glacial sediments while the inner bay has a sedimentation gradient along the coast with lower light and salinity and greater inorganic sedimentation at the head of the bay (Abookire et al., 2000; Spurkland and Iken, 2011). The counter-clockwise circulation carries some glacial fresh water and sediment westward along the bay's north shore toward the mouth (Gatto, 1982). Six sites at 10-m water depth were established to encompass the range of glacial exposure in Kachemak Bay (Fig. 1). Three sites were in the more oceanic outer bay (O1, O2, and O3) and three were in the glacially fed inner bay (I1, I2, and I3). These sites were chosen to visually have similar bottom slope and substrate composition. At each site, several components of the biological community and various environmental factors associated with glacial melt were sampled.

2.2. Sampling of recruitment of the sessile community and of mobile invertebrates and adult kelp over time

Six bare slate rocks were placed at each site to estimate recruitment of the sessile community (invertebrates and macroalgae) and the presence of mobile invertebrates over time. For this, 72 rocks were collected from two intertidal sites located mid-bay (Kasitsna Bay and Jakolof Bay). The rocks were scraped clean with a wire brush, placed in the sun for 48 h to eliminate any spore bank, and individually tagged with white-out paint. All rocks were approximately 5 cm thick, 25 cm wide and 35 cm long with two flat surfaces, one facing down to ensure that the rock did not roll and one facing up for settlement. Six rocks were randomly assigned to each site. Rocks were haphazardly placed along a 10-m permanent transect along the 10-m isobath at mean lower-low water marked with a plastic-coated steel cable.

Percent cover was visually estimated for all recruiting sessile invertebrates and macroalgae. Individual kelp were also counted and pictures were taken of the rocks so that rock area could be calculated using Image J (Schneider et al., 2012). Counts were standardized to rock surface area by dividing the raw count by the surface area. The first set of rocks was deployed in March 2013. A subsequent set was deployed in April 2014 to examine temporal variability in recruitment and colonization. After deployment, all rocks were surveyed in April of both years, and biweekly from May to September in 2013 and 2014 using SCUBA. No surveys were conducted from October to March due to inclement weather. Initial recruitment and colonization were examined over the first 1–6 months for rocks deployed in 2013 and 2014 and from 12 to 18 months for the rocks deployed in March 2013.

At each site, the density of small mobile invertebrates (such as limpets and chitons) was monitored by counting all individuals present on each experimentally cleared rock. These small invertebrates were identified to the lowest taxonomic level possible in the field (usually to class or lower). Counts were standardized to rock surface area by dividing the raw count by the surface area and expressed as density per m².

Larger invertebrates (e.g., sea stars such as *Asterias amurens*) and adult kelp were counted along two haphazardly-placed replicate 2 × 10-m transects at each site. Transects started 1 m from each end of the permanent transect where cleared rocks were placed and the direction of each transect was chosen haphazardly. All invertebrates and kelp along these transects were identified to the lowest taxonomic level possible. Fish were not surveyed because of the logistical challenges of visual surveys in low visibility conditions.

2.3. Environmental factors

At each site, environmental factors directly related to glacial discharge were monitored, including sedimentation rate, bottom water temperature, irradiance, salinity, and nutrient concentrations [nitrate (NO₃⁺), ammonium (NH₄⁺), phosphate (PO₄³⁻), and silicate (SiO₄²⁻)]. Sediment traps were used to determine sedimentation rates at each site from March to September 2013 and April to September 2014. These traps consisted of three polyvinyl chloride pipes with a height: diameter ratio of 5:1 to prevent resuspension (Hargrave and Burns, 1979) and were placed with the mouth of the trap approximately 0.7 m above the bottom. Once per month, traps were retrieved and replaced with new ones. Particulate mass flux was quantified by filtering the trap samples onto pre-weighed Whatman GF/F glass microfiber filters (0.7 µm). Filters were dried for 24 h at 60 °C to obtain dry weight. Filters were then burned for 6 h at 500 °C and re-weighed to determine organic content as the ash-free dry weight. Inorganic content was estimated as the remaining content after the organic content was burned off.

Bottom temperature and irradiance (photon intensity per area) were recorded hourly at each site using Honest Observer by Onset (HOBO) Pendant data loggers (Onset Computers, Bourne, Massachusetts) fixed

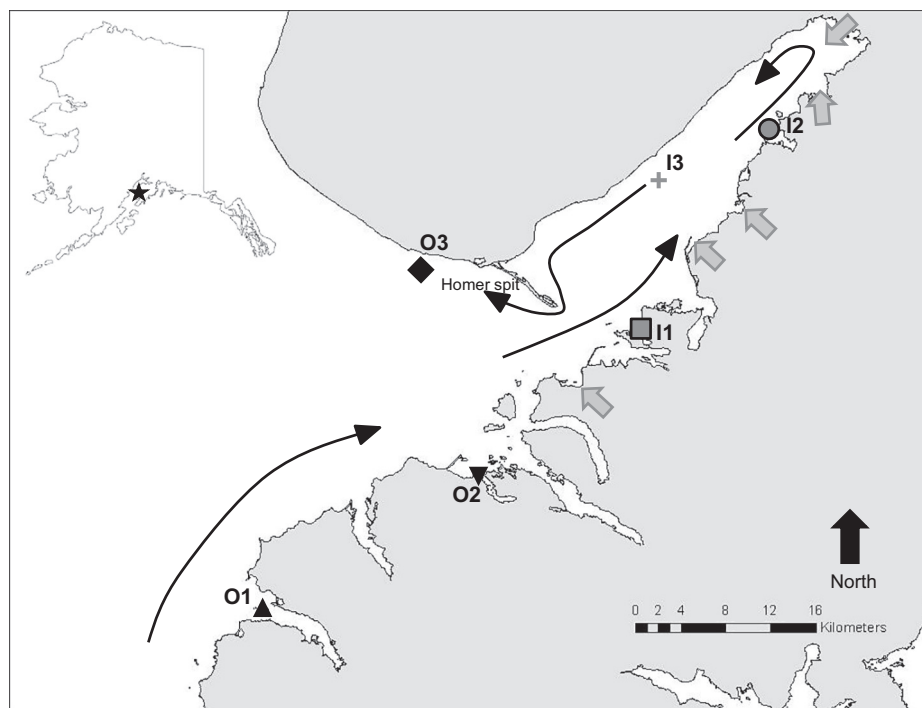


Fig. 1. Map of Kachemak Bay showing study sites. The black star on the inset map shows the location of the study area within Alaska. The Homer spit divides the bay into the outer (black symbols) and inner (gray symbols) regions. Study sites are Port Graham (O1), Jakolof Bay (O2), Bishop's Beach (O3), Peterson Bay (I1), Bear Cove (I2), and McNeil Canyon (I3). Black arrows show circulation patterns. Gray arrows show freshwater and glacial point discharges.

to cinderblocks on the sea floor. Two-week averages of temperature and irradiance were calculated from daily averages of the hourly data. For irradiance, data points between sunset and sunrise were excluded. The maximum and minimum temperature and maximum irradiance value within each two-week period were also included as variables in our analysis. Minimum irradiance was not used because the minimum irradiance was always zero. Due to loss of data loggers, no data are available for some of the outer sites (O1 in 2013 and O2 and O3 from July to September 2013).

Bottom salinity was measured with a hand-held multi-parameter instrument (Yellow Springs Instruments ProPlus, Yellow Springs Instrument Company, Yellow Springs, Ohio) at each site and each sampling event in 2013. In 2014, salinity was monitored hourly with HOBO conductivity U24 data loggers (Onset Computers, Bourne, Massachusetts) fixed to cinderblocks next to the light and temperature loggers at each site. Two-week averages of the daily average salinity data from 2014 were used in the analysis. Maximum and minimum salinity in each two week period was compared to long-term colonization (2014 data). Only mean salinity was compared to 1–6 month colonization because maximum and minimum salinities were not available; only one salinity measurement was taken at each site and each sampling event in 2013.

For nutrient analysis, water samples were collected from less than 1 m above the bottom at each site on each visit. Water samples were filtered with Nalgene syringe filters (0.45 μm) within 1 h of collection and transported back to the lab in a cooler with ice. Water samples were then frozen for up to five months until nutrient analysis. Nutrient samples were analyzed approximately one month after the last sample was taken, so samples collected earlier in the summer were frozen for longer than those collected at the end of the summer. Nitrate, ammonium, phosphate, and silicate were measured with a Technicon AutoAnalyzer II (SEAL Analytical Inc., Mequon, Wisconsin).

2.4. Data analysis

Multivariate analyses were carried out in PRIMER, a multivariate statistical software package (v7, Plymouth Marine Laboratories). Before statistical analyses, all variables in each data set were examined for

univariate correlations using draftsman plots (Clarke et al., 2014). Abundance of the sea star *Leptasterias hexactis* was deleted because of high correlations with other variables ($r > 0.95$, Clarke et al., 2014). Biological data were 4th-root transformed to prevent the most abundant organisms from dominating the analysis (McCune et al., 2002). Percent cover data were analyzed separately from kelp recruitment density data, so no standardization was needed. Environmental data (sedimentation rates, minimum and maximum temperature, mean and maximum light, salinity, nitrate, ammonium, phosphate, and silicate) were normalized by subtracting the mean and dividing by the standard deviation for each variable (Clarke et al., 2014).

PERMANOVA and SIMPER analyses were used to describe spatial differences in the biological community. Separate analyses were conducted on the sessile community that recruited onto the cleared rocks, the mobile invertebrate data sets, and the adult kelp transect data. Separate Bray-Curtis similarity matrices were generated from the multivariate percent-cover data from rocks deployed in March 2013 (except for site O2 where rocks were deployed in May) through September 2014, the mobile invertebrate density, and the adult kelp transect density. Percent cover data among replicate rocks were averaged at each site for each sampling event. Adult kelp transect data were averaged for the two replicate transects at each site and sampling event. The PERMANOVA design included Region (fixed, 2 levels: Outer Bay, Inner Bay), Site (random, nested in Region, 6 levels: O1, O2, O3, I1, I2, I3), Month (random, 6 levels: April, May, June, July, August, September), and Year (random, 2 levels: 2013, 2014). To account for the repeated measures aspect of the study design for the percent cover recruitment data, the number of months rocks were deployed was included as a covariate and designated as “Age.” SIMPER analysis was used to determine species that contributed to similarity within each site and constructed time series plots to visualize changes in percent cover over time for the most important species. PERMANOVA analysis based on Euclidean distance and Principal Component Analysis (PCA) were used to describe spatial and temporal variation in environmental data.

Distance-based linear models (DistLM) were used to determine the importance of environmental factors for affecting each biological community data set. “Age” was included as an ordinal variable available for the model to select for the analysis with cleared rocks. Step-

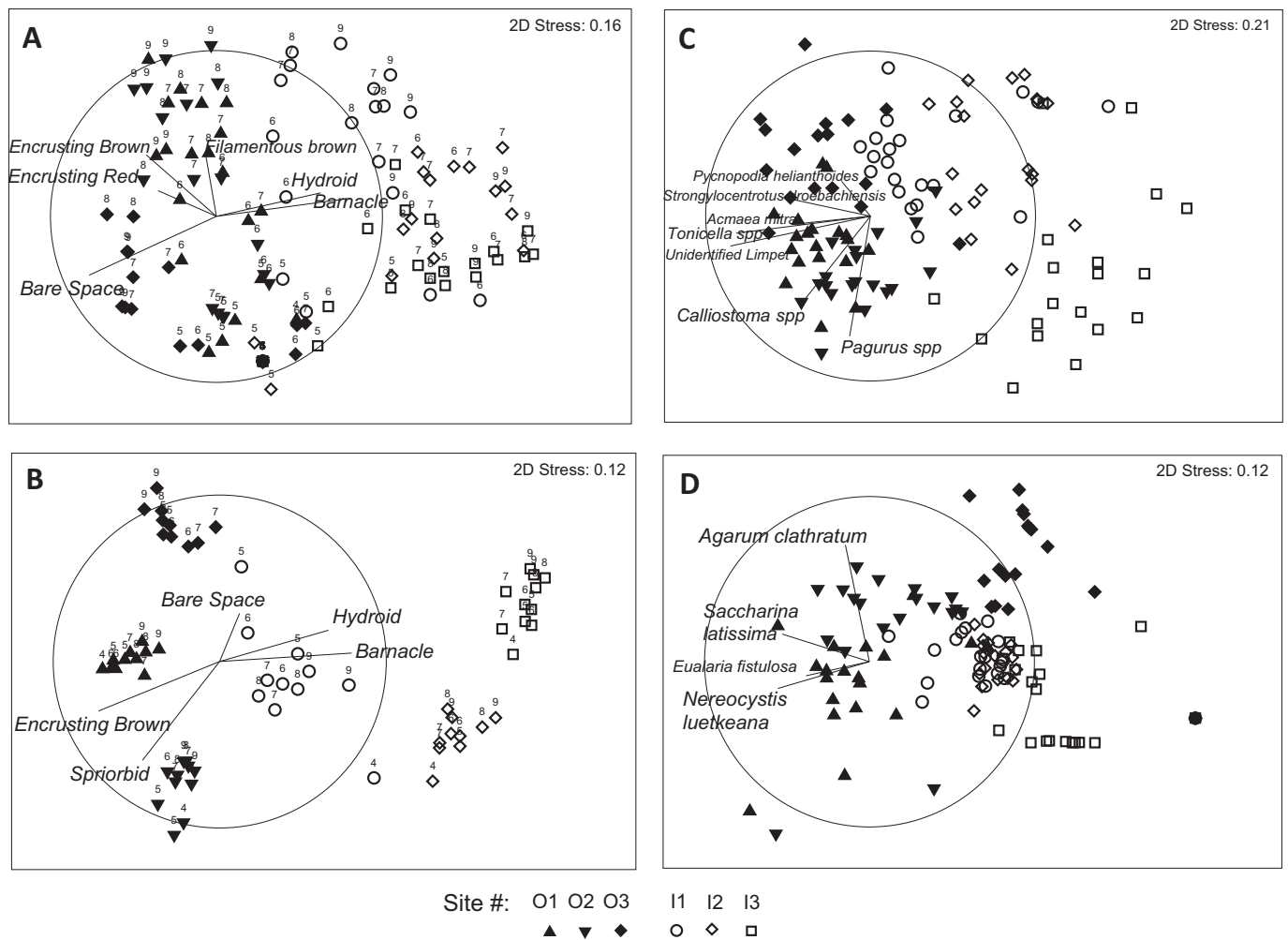


Fig. 2. Community structure in each data set represented in non-metric multidimensional scaling plot using bray Curtis similarity matrix: A) sessile communities after 1–6 months, B) sessile communities 12–18 months, C) mobile invertebrates, and D) adult kelp in surrounding community. In panel A and B, numbers above the data points are months (5: May, 6: June, 7: July, 8: August, 9: September). Vectors are shown for taxa that contributed to similarity within regions. Site abbreviations as in Fig. 1.

wise selection procedure and adjusted R^2 selection criteria were used.

3. Results

3.1. Patterns of sessile community colonization, mobile invertebrates and adult kelp abundance over time

There were clear differences in initial recruitment and early colonization over the first six months between the inner bay and outer bay regions (Figs. 2A, B, 3). The two regions differed in the composition of early colonizers (Table 1). Species that contributed to similarity within the outer bay included spirorbid worms, encrusting brown and red algae, and filamentous brown algae (Table 2A). Bare space was abundant at outer bay sites for the first six months after rocks were deployed, while percent cover of encrusting brown and red algae and filamentous brown algae gradually increased in the early summer (Table S1). In the inner bay, barnacles quickly colonized rocks, resulting in a decline in availability of bare space (Table S1). Barnacles and hydroids contributed to similarity within the inner bay (Table 2B), while these were largely absent from the outer bay. Kelp recruits appeared at site O1 in June and O2 in July, while no kelp recruits appeared at O3 (Table S2). Kelp recruits appeared in July at I1, in May at I2, and no kelp recruits appeared at I3 (Table S2). Juvenile *Saccharina latissima* occurred at O1, O2, and I1. Juvenile *Agarum clathratum* occurred at O1 and O2. Juvenile *Laminaria yezoensis* occurred at O1. Even after variability due to

“Age” was partitioned, there were still significant effects of region (Table 1, $P = 0.003$), and site nested within region (Table 1, $P = 0.005$). Colonization over time differed between regions and among sites, as indicated by the significant interaction between “Age” and these factors (Table 1).

In the second summer of colonization (12–18 months after rocks were deployed) differences in community structure among sites became more apparent with less distinction between regions (Fig. 2B). This can be seen from the tight clustering of data points by site on the MDS (Fig. 2B) and the larger *Pseudo-F* value associated with site (region) than region (Table 3). During this time period, there was no longer a significant effect of the “Age” covariate (Table 3). However, some sites were more variable over time than others, which is reflected by the spread of points within sites in Fig. 2B and the significant interaction of “Age” and sites (region) (Table 3). The number of species contributing to similarity was higher in both regions over the 12–18 month time period than the 1–6 month period. In the outer bay, encrusting brown algae and spirorbid worms were again among the most important contributors to similarity (Table 4A). Percent cover of these groups remained similar through this time in the outer bay (Table S3). O3 in the outer bay, located on the northern side of Kachemak Bay, varied from the other two outer bay sites in the high availability space during this period. This can be seen by the placement of the O3 data points near the top of the plot where the vector for bare space indicates high availability of bare space (Fig. 2B). As in the 1–6 month period,

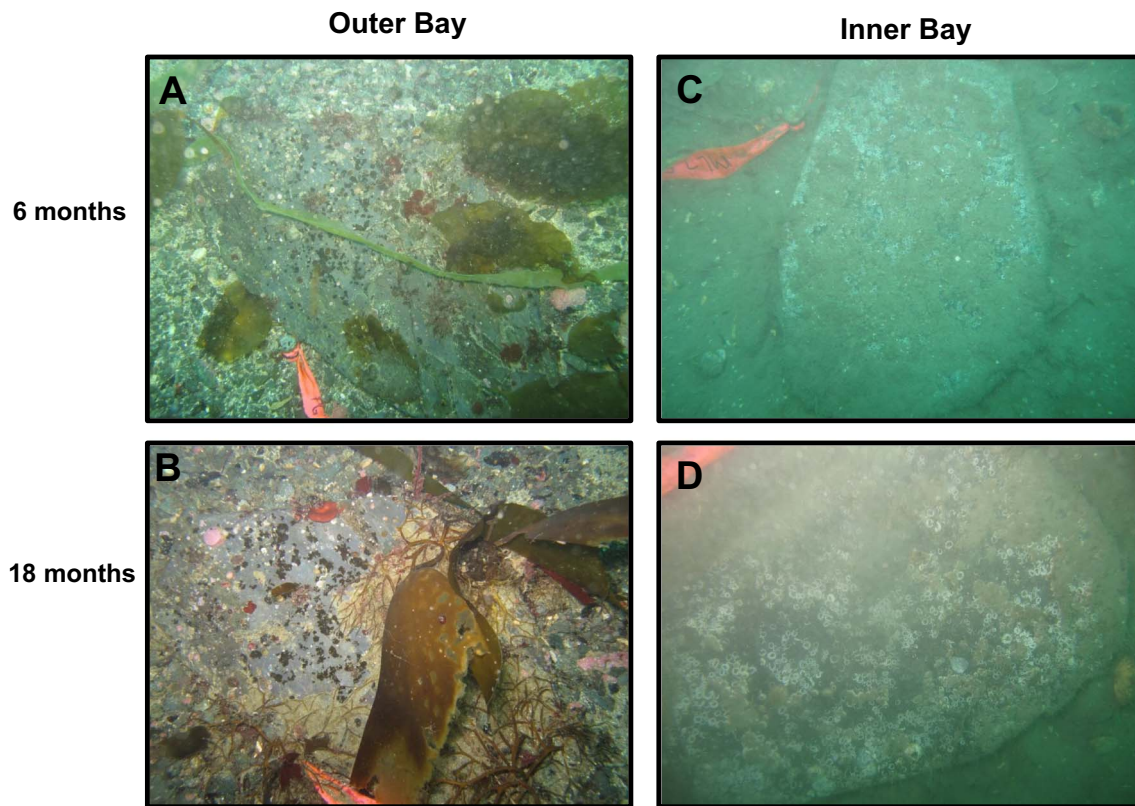


Fig. 3. Examples of sessile communities on rocks A) in the outer bay after 6 months, B) in the outer bay after 18 months, C) in the inner bay after 6 months, and D) in the inner bay after 18 months.

Table 1

Results of a PERMANOVA comparing community structure over 1–6 months between regions (fixed, two levels), among sites nested within regions (random, six levels), months (random, five levels: May, June, July, August, and September), and years (random, two levels: 2013 and 2014). “Age” was included as a covariate. Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	df	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	25,156	25,156	14.405	0.0021
Region	1	35,464	35,464	3.9234	0.0027
Month	5	7675.7	1535.1	1.3829	0.2047
Year	1	3878.2	3878.2	2.294	0.0861
Site (region)	4	18,596	4649	3.372	0.0048
Age × region	1	6899.8	6899.8	6.4239	0.0119
Age × site (region)	4	4057.3	1014.3	3.1206	0.0021
Region × month	5	4403.5	880.7	1.0115	0.4915
Region × year	1	1720.9	1720.9	1.458	0.2532
Site (region) × year	4	1944.2	486.05	1.8956	0.0747
Res	26	5246.7	201.8		
Total	117	0.00001			

barnacles and hydroids were among the most important contributors to similarity within the inner bay (Table 4B). I1 in the inner bay had lower cover of barnacles, and this can be seen in Fig. 2B by the placement of these data points closer to the outer bay sites where barnacles were absent or very rare (Fig. 2B). Kelp was more abundant at the outer bay than inner bay (Table S4). *Saccharina latissima* and *A. clathratum* grew to adult size at sites where they occurred. In contrast to sites O1 and O2, only one kelp recruit occurred at O3, which became identifiable as a juvenile *A. clathratum* in late summer. Only two *Nereocystis luetkeana* appeared at site O1 and these only survived for one month.

Abundance of both smaller and larger mobile invertebrates differed between the outer and inner bay (Fig. 2C, Table S5). Unidentified limpets contributed 40% to similarity within the outer bay and were the

Table 2

Percent contribution (Contrib.) of discriminating species for community structure over 1–6 months in each region using SIMPER analysis. Average percent cover (\pm SD) and cumulative percent contribution to similarity (Cum.).

	Average % cover \pm SD	Contrib.	Cum.
Outer bay			
Bare space	92.7 \pm 9.5	72.96	72.96
Spirorbis	3.2 \pm 4.6	8.80	81.76
Encrusting brown algae	1.4 \pm 2.7	4.43	86.19
Encrusting red algae	0.3 \pm 0.6	2.38	88.57
Filamentous brown algae	0.9 \pm 2.7	2.04	90.60
Inner bay			
Bare space	61.5 \pm 31.0	60.00	60.00
Barnacle	31.9 \pm 32.2	24.11	84.11
Hydroid	2.0 \pm 2.3	8.90	93.01

Table 3

Results of a PERMANOVA comparing community structure over 12–18 months between regions (fixed, two levels), among sites nested within regions (random, six levels), and months (random, five levels: May, June, July, August, and September). “Age” was included as a covariate. Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	df	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	6200.6	6200.6	2.9578	0.1912
Region	1	34,233	34,233	3.4634	0.0059
Month	5	9703	1940.6	1.006	0.4769
Site (region)	4	31,697	7924.3	23.247	0.0001
Age × region	1	483.7	483.7	4.1022	0.0962
Age × site (region)	4	3026.9	756.72	2.595	0.0291
Region × month	5	493.81	98.763	0.29901	0.978
Total	63	93,448			

Table 4
Percent contribution (Contrib.) of discriminating species for community structure over 12–18 months in each region using SIMPER analysis. Average percent cover (\pm SD) and cumulative percent contribution to similarity (Cum.).

	Average % cover \pm SD	Contrib.	Cum.
Outer bay			
Bare space	60.7 \pm 19.3	27.08	27.08
Encrusting brown algae	9.5 \pm 4.9	15.38	42.46
Spirorbid	9.5 \pm 9.7	12.09	54.55
Crustose coralline	6.3 \pm 11.8	9.61	64.16
Unidentified polychaetes	1.3 \pm 1.2	9.01	73.17
<i>Saccharina latissima</i>	1.9 \pm 2.2	4.31	77.48
Kelp recruits	2.0 \pm 4.1	3.62	81.10
Unidentified sand-tube polychaete	1.3 \pm 1.4	3.54	84.64
Encrusting red algae	1.4 \pm 2.7	2.32	86.97
<i>Agarum clathratum</i>	0.4 \pm 0.6	2.29	89.25
Filamentous red algae	1.6 \pm 3.5	1.30	90.55
Inner bay			
Bare space	76.1 \pm 15.3	39.49	39.49
Barnacle	11.7 \pm 11.4	13.43	52.92
Hydroid	4.8 \pm 6.9	9.77	62.70
Filamentous red algae	1.3 \pm 1.5	7.28	69.98
<i>Saccharina latissima</i>	0.9 \pm 0.8	6.21	76.19
Kelp recruits	0.3 \pm 0.3	4.63	80.81
Filamentous brown algae	1.2 \pm 2.2	3.08	83.89
<i>Metridium</i> spp.	0.6 \pm 0.9	2.65	86.54
Brown tube polychaete	1.0 \pm 2.4	1.74	88.27
Peach bryozoan	0.3 \pm 0.4	1.50	89.77
Red blades	0.2 \pm 0.3	1.47	91.24

most abundant herbivores (Fig. 2C, Table S6). Other mobile invertebrates including the chiton *Tonicella* spp., and the green sea urchin *Strongylocentrotus droebachiensis* were also more abundant in the outer bay region. The sea star *Asterias amurensis* only occurred at inner bay sites.

The adult kelp assemblage surveyed in transects differed between the outer bay and the glacially-influenced inner bay region (Fig. 2D, Table S7). Abundance of kelp was generally higher in the outer bay (Table S8). The understory kelps, *A. clathratum* and *S. latissima* contributed to similarity within both regions and were more abundant in the outer bay (Table S8). The canopy-forming kelps, *N. luetkeana* and *Eualaria fistulosa* were never observed in the inner bay or at site O3.

3.2. Environmental factors

Glacially influenced environmental factors were significantly different among months (Table S9). The PCA reflects the PERMANOVA by

showing clear separation of data points among months (Fig. 4A). Maximum temperature and mean salinity showed seasonal changes in both regions (Table S10). Maximum temperature increased from May to September and salinity declined in late summer (Fig. 4A). There was high variability in inorganic and organic sedimentation rates, though rates were highest in late summer for the inner bay region (Table S10). Phosphate concentration increased slightly at the end of the summer at both regions (Table S10, Fig. 4A).

In contrast, regions were not clearly distinguished by environmental factors (Table S9, Fig. 4B) although there were significant differences in environmental factors among some sites (Table S11). There were significant differences in environmental conditions between the most upstream site, site O1, and all inner bay sites (Table S11B). Site O2, on the southern side of the outer bay was only significantly different from site I3, a downstream site (Table S11B). Although overall environmental conditions were not significantly different between the outer and inner bay regions, some differences in variables were apparent between regions over time. Inorganic sedimentation rates were almost always higher at the inner bay sites (Fig. 5). The exceptions to this pattern are in May 2013, where inorganic sedimentation rates at O1 were unusually high and for site O3, which occasionally had high rates of inorganic sedimentation (Fig. 5). Correspondingly, irradiance was almost always lower at the inner bay region than the outer bay region (Table S10). Concentration of silicate tended to be higher in the outer bay earlier in the summer, while ammonium concentration tended to be higher in the inner bay later in the summer (Table S10).

3.3. Biological correlations with environmental factors

Colonization in the first summer that rocks were deployed (1–6 months) was most strongly correlated to maximum temperature, followed by inorganic sedimentation rate, and mean temperature. These three variables together explained 46.3% of the variation in the recruited rock communities (Table 5B). Organic sedimentation also explained 4.1% of the variation (Table 5A). The “Age” factor also explained a small amount of the variation (Table 5A). Correlations with temperature and rock “Age” is likely related to the seasonal increase in overall percent cover of organisms on the rocks. Variation in rock colonization in the second summer (12–18 months) was related to inorganic sedimentation explaining 29.5% of variation (Table 5B).

DistLM analysis was additionally performed with kelp recruit density (including unidentified recruits < 2 cm in length) in the first summer (1–6 months). Variation in kelp recruit density was related to maximum irradiance ($Pseudo-F = 7.6674$, $P = 0.011$, variation explained = 16.1%). DistLM analysis was also conducted on density of

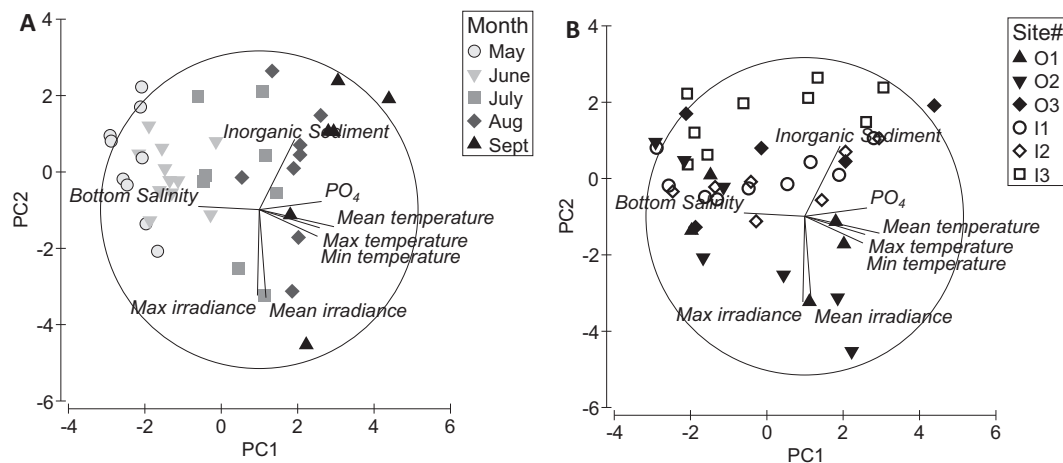


Fig. 4. Principal components analysis of environmental variables with data points coded by A) Month and B) Site. Vectors are shown for variables with correlations < -0.3 or > 0.3 with PC1 or PC2. Site abbreviations as in Fig. 1.

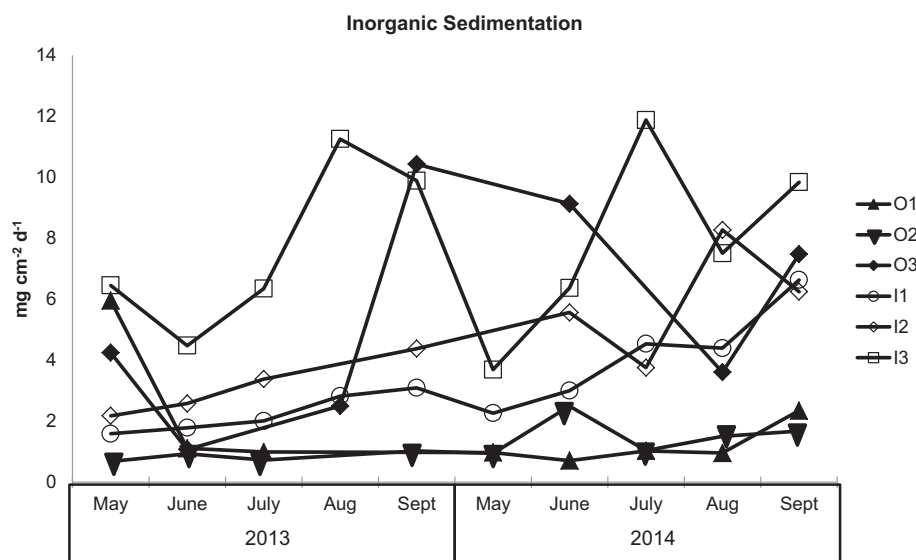


Fig. 5. Inorganic sedimentation rates at each site over time. Points represent values averaged between replicate sediment traps. Standard deviation is not shown here for simplicity. Site abbreviations as in Fig. 1.

Table 5

Results of sequential DistLM tests on A) first year (1–6 months) of community structure, B) second year (12–18 months) of community structure, C) adult kelp from transects, and D) mobile invertebrates showing significant variables, their contribution to explained variation (Contrib.), the cumulative contribution of the explained variation (Cum.) and *P*-values.

	<i>Pseudo-F</i>	Contrib.	Cum.	<i>P</i> -value
A) First year community structure				
Max. temperature	9.428	19.1	19.1	0.001
Inorganic sedimentation	6.997	12.3	31.4	0.001
Mean temperature	10.525	14.9	46.3	0.001
Organic sedimentation	3.4714	4.1	55.0	0.012
Age	3.303	2.2	57.1	0.017
B) Second year community structure				
Inorganic sedimentation	10.457	29.5	29.5	< 0.001
C) Mobile invertebrates				
Inorganic sedimentation	6.515	14.0	14.0	< 0.001
SiO ₄	4.365	8.7	22.7	0.001
NH ₄	3.888	7.2	29.8	0.002
D) Adult kelp from transects				
Inorganic sedimentation	13.751	25.6	25.6	< 0.001
SiO ₄	3.976	6.9	32.5	0.017

kelp that occurred on cleared rocks during the 12–18 month period. This included unidentified kelp recruits (< 2 cm in length), *S. latissima*, *A. clathratum*, *L. yezoensis*, *Cymathaea triplicata*, and *N. luetkeana*. Variation in kelp density on rocks was best correlated to maximum irradiance (*Pseudo-F* = 11.129, *P* = 0.001, variation explained 30.8%), “Age” (*Pseudo-F* = 3.157, *P* = 0.027, variation explained = 8.0%), mean temperature (*Pseudo-F* = 5.126, *P* = 0.001, variation explained = 11.1%), and inorganic sedimentation rate (*Pseudo-F* = 3.126, *P* = 0.033, variation explained = 6.2%).

Inorganic sedimentation rate was the variable most strongly correlated to mobile invertebrate and adult kelp distribution (Table 5C, D). Inorganic sedimentation explained 14.0% of variation in the mobile invertebrate assemblage, followed by silicate concentration (8.7%) and ammonium concentration (7.2%, Table 5C). Inorganic sedimentation explained 25.6% of variation in adult kelp abundance, followed by silicate concentration which explained 6.9% (Table 5D).

4. Discussion

Monitoring initial recruitment and colonization by sessile communities can help to form hypotheses about successional processes in kelp beds. Kelp bed community recruitment and development in the

glacially influenced estuary examined in this study differed between the oceanic-influenced outer region and the glacially-influenced inner region. The most abundant members of the recruiting communities were spirorbid worms and macroalgae in the outer bay and barnacles in the inner bay. This is similar to patterns of macroalgal abundance in relation to sedimentation in Ireland (Maughan, 2001), the Mediterranean (Balata et al., 2007), and Norway (Bogen, 2009). Our observations of higher cover of hydroids in the inner bay agrees with an experimental study finding that sessile organisms with upright growth forms, including hydroids were unaffected by sedimentation (Houle, 2015). Similar to high sediment coastal lagoons in south Texas, we observed high barnacle recruitment despite the presence of sediment (Gray, 2014). Shifts between algal and invertebrate-dominated communities have also been observed in Antarctica when changes in sea ice affected sedimentation and light conditions (Clark et al., 2017).

Similar to other high-latitude studies, in this study bare space was colonized slowly (Barnes and Conlan, 2007; Konar, 2007). Although most kelp and red macroalgal species are reproductive during early summer in Kachemak Bay (personal observation), kelp recruitment was slow and not observed until two to three months after rocks were deployed (Table S1). This may be because kelp gametophytes can delay reproduction and production of macroscopic sporophytes until they are triggered by changing environmental factors such as light or nutrients (Carney and Edwards, 2006). Slow substrate colonization in high latitude systems compared to temperate systems has been reported previously (Barnes and Conlan, 2007). For example, in an Arctic boulder field, experimentally cleared boulders still had over 90% bare space after 3 years (Konar, 2007). In contrast, recovery of kelp cover over several weeks has been observed in experimental and natural clearings at lower latitudes (Barradas et al., 2011; Dayton et al., 1992). In many systems, following a disturbance, typical succession process includes early opportunists followed by later slower growing species. In rocky temperate intertidal systems, early opportunists can include *Ulva* spp. and filamentous algae, which may be later replaced by slower growing red macroalgae (Aquilino and Stachowicz, 2012; Kraufvelin et al., 2007). In our system, the early opportunists were spirorbid worms and barnacles. Spirorbid worms are also abundant early colonizers in highly disturbed subtidal habitats in Antarctica (Barnes and Conlan, 2007).

Competitive interactions among early recruits to bare space may be stronger in the inner bay region with high barnacle recruitment than at the outer bay. Recruitment rates varied among our sites with barnacles quickly colonizing bare space in the inner bay and with recruitment occurring much more slowly by spirorbid worms and macroalgae in the outer bay. Competition for space may not have been important in the

early stages of colonization in the outer bay where bare space was abundant during the first summer of the study. Preemptive competition among macroalgae has been shown to be an important structuring mechanism of communities in other systems. For example, in littoral rock pools in Italy, turf forming algae and *Cystoseira* spp. have non-hierarchical competitive interactions where whichever group is present in higher density can exclude recruitment of the other group; however, when turf algae and *Cystoseira* spp. recruit at the same time, they can coexist (Benedetti-Cecchi and Cinelli, 1996). This type of competition between *Cystoseira* spp. and turf algae can be more important in shaping communities than storm disturbance (Maggi et al., 2012). Similarly, in subtidal kelp beds in Australia, dense mats of filamentous algae can preempt kelp recruitment (Connell and Russell, 2010). Hence, the availability of bare space and the availability of propagules can be crucial to the coexistence of species. Encrusting algae can inhibit kelp recruitment; however, kelp canopies can persist despite high cover of encrusting algae because kelp produce very high numbers of spores, which can settle in minute bare patches or on top of encrusting algae (Okamoto et al., 2013). Although there is strong evidence that space is limiting in many sessile communities (Benes and Carpenter, 2015; Gorman and Connell, 2009; Maggi et al., 2012), we should be cautious in our interpretation of high availability of bare space as an indication of low competition, as members of the sessile community may be competing for other limiting resources such as planktonic food (Svensson and Marshall, 2015).

Some glacially-influenced environmental factors were significantly correlated to patterns of recruitment and colonization. While many environmental factors were similar among sites, inorganic sedimentation differed with the highest rates at sites downstream of glacial discharge point sources. In addition, colonization in the first summer (1–6 months) was primarily driven by temperature and inorganic sedimentation while colonization in the second summer (12–18 months) was only correlated with inorganic sedimentation (Table 5A, B). Irradiance was correlated to kelp recruitment in the first and second summers. Our results agree with previous studies finding that sedimentation and irradiance are important factors structuring macroalgal communities (Bogen, 2009; Clark et al., 2017; Desmond et al., 2015). Low salinity can cause osmotic stress in recruiting barnacles, causing latent effects on growth and survival (Nasrolahi et al., 2013; Qiu and Qian, 1999). Sedimentation inhibits recruitment of spirorbid polychaetes (Connell, 2003). Kelp recruitment is negatively correlated to sedimentation rates (Spurkland and Iken, 2011; Valentine and Johnson, 2005) and sedimentation and low salinity decrease the success of *Nereocystis luetkeana* spore settlement and attachment (Deiman et al., 2012), and gametophyte survival and growth (Lind and Konar, 2017). Sediments can kill early macroalgal and invertebrate life stages through burial or smothering, scour, and changes in substrate stability (Airoldi, 2003). In southeastern Tasmania, kelp recruits transplanted to urchin barrens, where thick sediment layers accumulate, experienced high mortality, even when urchins were excluded (Valentine and Johnson, 2005). Irradiance was correlated to kelp abundance on rocks in this study. In some cases sedimentation can cause light limiting conditions for kelp (Desmond et al., 2015) but sediment can also protect kelp from high light (Roleda and Dethleff, 2011).

Similar to recruitment and colonization, the composition and abundance of mobile invertebrates and adult kelp differed between these two regions. Mobile invertebrates and adult kelp in the established community were more abundant in the oceanic-influenced outer bay. Some glacially-influenced environmental factors were significantly correlated to the surrounding community. For example, inorganic sedimentation was significantly correlated to mobile invertebrates and adult kelp. The identification of inorganic sedimentation as a potential driver of kelp and mobile invertebrate assemblage structure is supported by similar observations of differences in abundance in relation to sedimentation (Airoldi and Virgilio, 1998; Bogen, 2009) and experimental studies indicating that sedimentation can cause mortality of

kelp and invertebrates (Deiman et al., 2012; Geange et al., 2014; Kawamata et al., 2012; Walker, 2007). Sediment has been shown to directly affect the spatial distribution, survival, and grazing of limpets (Airoldi and Hawkins, 2007; Branch et al., 1990). Observed low mobile invertebrate abundances were associated with high rates of inorganic sedimentation at the glacially-influenced, inner bay sites. Mobile invertebrates may be more abundant upstream of glacial discharge due to lower sedimentation rates (Airoldi and Hawkins, 2007), or due to the higher abundance of kelp in the surrounding community that many mobile invertebrates feed on (Bustamante et al., 1995). *Tonicella* spp. also graze benthic diatoms (Latyshev et al., 2004), which may be more abundant at sites with low glacial influence.

The environmental conditions observed in this study were more spatially homogeneous than expected, which indicates that currents are important in spreading glacially-influenced water throughout Kachemak Bay. Our findings contrast previous work in Kachemak Bay, which found large differences in surface salinity, water column salinity stratification, temperature, irradiance, and nitrate concentrations between sites upstream and downstream of glacial discharge (Abookire et al., 2000; Spurkland and Iken, 2011). Conductivity temperature depth (CTD) profiles conducted at Halibut Cove, downstream of our site I1, showed that there is a halocline at 4-m depth, below which salinities are similar to those found in the outer bay (Schoch and Chenelot, 2004). In Kachemak Bay, Spurkland and Iken (2011) observed differences in salinity and irradiance at 5-m depth, but in this study, sites were at 10-m depth, so the low salinity, low temperature, low nitrate, high sediment water from glacial discharge, though present, may have reached the loggers or experimental rocks at the deeper depth only occasionally. Stratification may therefore partially protect subtidal kelp beds from glacial meltwater-related effects. Similarly, flooding of the Orange River in Africa caused high mortality of algae and invertebrates in the intertidal zone while the subtidal zone was not affected (Branch et al., 1990). Rates of inorganic sedimentation did follow spatial patterns similar to previous findings in this and other systems (Spurkland and Iken, 2011; Svendsen et al., 2002). Similar to the Kongsfjorden glacial fjord system in Svalbard, we observed a gradient in inorganic sedimentation with rates declining toward the mouth of the bay (Svendsen et al., 2002). Some of our sites (site I1 & O3) may be located at regions representing transitions between the outer bay oceanic conditions and the inner bay glacially-influenced conditions. Circulation patterns may help homogenize conditions around the bay by spreading glacial fresh water and sediment to the north shore of the outer bay. The incoming current from Cook Inlet on the southern side of the inner bay may mix with the fresher and more turbid waters of the inner bay, decreasing the glacial influence along the southern side of inner Kachemak Bay (i.e., site I1, Fig. 1). As glacial discharge increases with warming temperatures in the future, our expectations about locations to be affected by changing water conditions will be based on the extent of glacial influence, including sedimentation, possibly reaching tens of kilometers past point sources of glacial discharge (Svendsen et al., 2002; this study).

In addition to glacial melt, other factors are also likely important to the observed patterns in the biological community. We expected to see some similarities in early colonizers between upstream and downstream sites due to the common water mass that passes through the study area (Fig. 1), possibly resulting in a somewhat similar propagule pool reaching multiple sites; however, there were few early colonizers in common between sites upstream and downstream of glacial discharge. Spirorbid polychaetes were among the earliest colonizers at sites upstream of discharge while barnacles were early colonizers downstream of glacial discharge. Several processes could be responsible for this pattern. A hydrodynamic front located at the boundary of the inner and outer bay at Homer spit may concentrate larvae, leading to higher transport into the inner bay, as was observed for the decorator crab, *Oregonia gracilis* (Murphy and Iken, 2014). Concentration and net transport into the inner bay may explain the much higher abundance of

species with longer larval duration such as barnacles in the inner bay than was observed in the outer bay. Spirorbid worms, which were common upstream but not downstream of glacial discharge, brood their larvae (Knight-Jones et al., 1991), and presumably have shorter dispersal distance than many other marine invertebrates such as barnacles. Encrusting algae such as crustose corallines also have short dispersal distances (Opazo and Otaiza, 2007), so populations upstream of glacial discharge may not supply propagules to glacially-influenced sites. The abundance of adult kelp at each site also likely affected propagule supply to our experimental rocks and may have contributed to the observed differences in kelp recruitment between the inner and outer bay regions. Kelp have short dispersal distances (Gaylord et al., 2004) and experimentally increasing adult density or reproductive material can increase local recruitment (Fejtek et al., 2011; Hernandez-Carmona et al., 2000).

4.1. Implications

Glacial melt may have significant effects on kelp communities through impacts on recruitment, survival, and interactions among species. As glacial melt dynamics are altered by climate change, the influence of glacially-influenced environmental factors is likely to change. This study contributes to the body of evidence indicating that kelp are negatively affected by sedimentation and could be threatened by increased glacial melt with climate change (Spurkland and Iken, 2011; Zacher et al., 2016). Increased sedimentation rates have already been associated with decreased diversity and dominance of a few opportunistic species (Balata et al., 2007; Connell, 2007; Pratt et al., 2014). In Alaska and other high latitude systems, we can expect kelp beds to be negatively impacted by the spread or increase of glacial sediment (Zacher et al., 2016). Climate change may also cause the peak in glacial discharge to shift from late summer and early fall to earlier in the summer. A better understanding of how environmental variables impact recruitment and colonization may help predict the effects of changes in glacial melt dynamics on kelp bed communities. Globally, kelp beds naturally experience environmental disturbances and can be highly resilient. In California, kelp beds can be greatly thinned or eliminated by El Niño conditions of high temperature and low nutrients, but kelp can quickly recover when conditions return to normal (Dayton et al., 1992). Other environmental disturbances may result in phase shifts with more permanent effects. In Australia, coastal development led to reduced water quality (eutrophic and high sedimentation), causing a phase shift from kelp to turf algal dominated (Connell and Irving, 2008). It is critical to understand the impacts of changing environmental conditions on existing and developing kelp beds, as they provide important ecosystem services.

Compliance with ethical standards

We have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2017.12.016>.

References

- Abdullah, M.I., Fredriksen, S., Christie, H., 2017. The impact of the kelp (*Laminaria hyperborea*) forest on the organic matter content in sediment of the west coast of Norway. *Mar. Biol. Res.* 13, 151–160.
- Abookire, A.A., Piatt, J.F., Robards, M.D., 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuar. Coast. Shelf Sci.* 51, 45–59.
- Agüera, A., Schellekens, T., Jansen, J.M., Smaal, A.C., 2015. Effects of osmotic stress on predation behaviour of *Asterias rubens* L. *J. Sea Res.* 99, 9–16.
- Airolidi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol.* 41, 161–236.
- Airolidi, L., Hawkins, S.J., 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. *Mar. Ecol. Prog. Ser.* 332, 235–240.
- Airolidi, L., Virgilio, M., 1998. Responses of turf-forming algae to spatial variations in the deposition of sediments. *Mar. Ecol. Prog. Ser.* 165, 271–282.
- Aquilino, K.M., Stachowicz, J.J., 2012. Seaweed richness and herbivory increase rate of community recovery from disturbance. *Ecology* 93, 879–890.
- Balata, D., Piazzi, L., Cinelli, F., 2007. Increase of sedimentation in a subtidal system: effects on the structure and diversity of macroalgal assemblages. *J. Exp. Mar. Biol. Ecol.* 351, 73–82.
- Barnes, D.K., Conlan, K.E., 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philos. Trans. R. Soc. B* 362, 11–38.
- Barradas, A., Alberto, F., Engelen, A.H., Serrao, E.A., 2011. Fast sporophyte replacement after removal suggests banks of latent microscopic stages of *Laminaria ochroleuca* (Phaeophyceae) in tide pools in northern Portugal. *Cah. Biol. Mar.* 52, 435–439.
- Benedetti-Cecchi, L., Cinelli, F., 1996. Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. *Mar. Ecol. Prog. Ser.* 135, 145–161.
- Benes, K.M., Carpenter, R.C., 2015. Kelp canopy facilitates understory algal assemblage via competitive release during early stages of secondary succession. *Ecology* 96, 241–251.
- Billot, C., Engel, C.R., Rousvoal, S., Kloareg, B., Valero, M., 2003. Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel. *Mar. Ecol. Prog. Ser.* 253, 111–121.
- Bogen, J., 2009. The impact of environmental changes on the sediment loads of Norwegian rivers. *Catena* 79, 251–256.
- Branch, G.M., Eekhout, S., Bosman, A.L., 1990. Short-term effects of the 1988 Orange River floods on the intertidal rocky-shore communities of the open coast. *Trans. Roy. Soc. S. Afr.* 47, 331–354.
- Bustamante, R.H., Branch, G.M., Eekhout, S., 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76, 2314–2329.
- Carnell, P.E., Keough, M.J., 2014. Spatially variable synergistic effects of disturbance and additional nutrients on kelp recruitment and recovery. *Oecologia* 175, 409–416.
- Carney, L.T., Edwards, M.S., 2006. Cryptic processes in the sea: a review of delayed development in the microscopic life stages of marine macroalgae. *Algae* 21, 161–168.
- Clark, G.F., Stark, J.S., Palmaer, A.S., Riddle, M.J., Johnston, E.L., 2017. The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. *PLoS One* 12, e0168391.
- Clarke, K.R., Gorley, R.N., Sommerfield, P.J., Warwick, R.M., 2014. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 3rd edition. PRIMER-E, Plymouth.
- Connell, S.D., 2003. Negative effects overpower the positive of kelp to exclude invertebrates from the understory community. *Oecologia* 137, 97–103.
- Connell, S.D., 2007. Water quality and the loss of coral reefs and kelp forests: alternative states and the influence of fishing. In: Connell, S.D., Gillanders, B.M. (Eds.), *Marine Ecology*, vol. 21. Oxford University Press, Sydney, Australia, pp. 556–568.
- Connell, S.D., Irving, A.D., 2008. Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *J. Biogeogr.* 35, 1608–1621.
- Connell, S.D., Russell, B.D., 2010. The direct effect of increasing CO₂ and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proc. R. Soc.* 277, 1409–1415.
- Dayton, P.K., Tegner, M.J., Parnell, P.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.
- Deiman, M., Iken, K., Konar, B., 2012. Susceptibility of *Nereocystis luetkeana* (Laminariales, Ochrophyta) and *Eualaria fistulosa* (Laminariales, Ochrophyta) spores to sedimentation. *Algae* 27, 115–123.
- Desmond, M.J., Pritchard, D.W., Hepburn, C.D., 2015. Light limitation within southern New Zealand kelp forest communities. *PLoS One* 10, e0123676.
- Duggins, D.O., Gomez-Buckley, M.C., Buckley, R.M., Lowe, A.T., Galloway, A.W.E.,

- Dethier, M.N., 2016. Islands in the stream: kelp detritus as faunal magnets. *Mar. Biol.* 163, 17–27.
- Eddy, E.N., Roman, C.T., 2016. Relationship between epibenthic invertebrate species assemblages and environmental variables in Boston Harbor's intertidal habitat. *Northeast. Nat.* 23, 45–66.
- Eftird, T.P., Konar, B., 2014. Habitat characteristics can influence fish assemblages in high latitude kelp forests. *Environ. Biol. Fish.* 97, 1253–1263.
- Fejtek, S.M., Edwards, M.S., Kim, K.Y., 2011. Elk kelp, *Pelagophycus porra*, distribution limited due to susceptibility of microscopic stages to high light. *J. Exp. Mar. Biol. Ecol.* 396, 194–201.
- Filbee-Dexter, K., Feehan, C.J., Scheibling, R.E., 2016. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar. Ecol. Prog. Ser.* 543, 141–152.
- Fredersdorf, J., Muller, R., Becker, S., Wiencke, C., Bischof, K., 2009. Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (phaeophyceae). *Oecologia* 160, 483–492.
- Gagnon, P., Johnson, L.E., Himmelman, J.H., 2005. Kelp patch dynamics in the face of intense herbivory: stability of *Agarum clathratum* (Phaeophyta) stands and associated flora on urchin barrens. *J. Phycol.* 41, 498–505.
- Gatto, L.W., 1982. Ice distribution and winter surface circulation patterns, Kachemak Bay, Alaska. *Remote Sens. Environ.* 12, 421–435.
- Gaylord, B., Reed, D.C., Washburn, L., Raimondi, P.T., 2004. Physical – biological coupling in spore dispersal of kelp forest macroalgae. *J. Mar. Syst.* 49, 19–39.
- Geange, S.W., Powell, A., Clemens-Seely, K., Cárdenas, C.A., 2014. Sediment load and timing of sedimentation affect spore establishment in *Macrocystis pyrifera* and *Undaria pinnatifida*. *Mar. Biol.* 161, 1583–1592.
- Gorman, D., Connell, S.D., 2009. Recovering subtidal forests in human-dominated landscapes. *J. Appl. Ecol.* 46, 1258–1265.
- Gray, J.J., 2014. Sedimentation and Barnacle Recruitment and Growth in a Shallow Coastal Lagoon of South Texas. University of Texas (Masters Thesis).
- Hamilton, J., Konar, B., 2007. Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities. *Fish. B-NOAA* 105, 189–196.
- Hargrave, B.T., Burns, N.M., 1979. Assessment of sediment trap collection efficiency. *Limnol. Oceanogr.* 24, 1124–1136.
- Hargrave, M.S., Foggo, A., Pessarrodona, A., Smale, D.A., 2017. The effects of warming on the ecophysiology of two co-existing kelp species with contrasting distributions. *Oecologia* 183, 531–543.
- Held, M.B.E., Harley, C.D.G., 2009. Responses to low salinity by the sea star *Pisaster ochraceus* from high- and low-salinity populations. *Invertebr. Biol.* 128, 381–390.
- Hernandez-Carmona, G., Gracia, O., Robledo, D., Foster, M., 2000. Restoration techniques for *Macrocystis pyrifera* (Phaeophyceae) populations at the southern limit of their distribution in Mexico. *Bot. Mar.* 43, 273–284.
- Holen, D., Evans, S., Kostick, M., Jones, B., 2012. The subsistence harvest of herring spawn on kelp in the Togiak District, Alaska, 2011 and 2012. In: Alaska Department of Fish and Game, Division of Subsistence, Special Publication No. BOF 2012-06.
- Houle, K.C., 2015. The Effects of Suspended and Accreted Sediment on the Marine Invertebrate Fouling Community of Humboldt Bay. Humboldt State University (Masters Thesis).
- Karsten, U., 2007. Salinity tolerance of Arctic kelps from Spitsbergen. *Phycol. Res.* 55, 257–262.
- Kawamata, S., Yoshimitsu, S., Tokunaga, S., Kubo, S., Tanaka, T., 2012. Sediment tolerance of *Sargassum* algae inhabiting sediment-covered rocky reefs. *Mar. Biol.* 159, 723–733.
- Knight-Jones, P., Knight-Jones, E.W., Buzhinskaya, G., 1991. Distribution and inter-relationships of northern spiroboid genera. *Bull. Mar. Sci.* 48, 189–197.
- Konar, B., 2007. Recolonization of a high latitude hard-bottom nearshore community. *Polar Biol.* 30, 663–667.
- Konar, B., Iken, K., 2005. Competitive dominance among sessile marine organisms in a high Arctic boulder community. *Polar Biol.* 29, 61–64.
- Kraufvelin, P., Ruuskanen, A.T., Nappu, N., Kiirikki, M., 2007. Winter colonisation and succession of filamentous macroalgae on artificial substrates and possible relationships to *Fucus vesiculosus* settlement in early summer. *Estuar. Coast. Shelf Sci.* 72, 665–674.
- Ladah, L.B., Zertuche-Gonzalez, J.A., 2007. Survival of microscopic stages of a perennial kelp (*Macrocystis pyrifera*) from the center and the southern extreme of its range in the Northern Hemisphere after exposure to simulated El Niño stress. *Mar. Biol.* 152, 677–686.
- Latyshev, N.A., Khardin, A.S., Kasyanov, S.P., Ivanova, M.B., 2004. A study on the feeding ecology of chitons using analysis of gut contents and fatty acid markers. *J. Molluscan Stud.* 70, 225–230.
- Lind, A., Konar, B., 2017. Effects of rising sea surface temperature and decreasing salinity on kelps and associated macroalgal communities. *Algae* 32 (3), 223–233.
- Mabin, C.J.T., Gribben, P.E., Fischer, A., Wright, J.T., 2013. Variation in the morphology, reproduction and development of the habitat-forming kelp *Ecklonia radiata* with changing temperature and nutrients. *Mar. Ecol. Prog. Ser.* 483, 117–131.
- Maggi, E., Bulleri, F., Bertocci, I., Benedetti-Cecchi, L., 2012. Competitive ability of macroalgal canopies overwhelms the effects of variable regimes of disturbance. *Mar. Ecol. Prog. Ser.* 465, 99–109.
- Markel, R.W., Shurin, J.B., 2015. Indirect effects of sea otters on rockfish (*Stebates* spp.) in giant kelp forests. *Ecology* 96, 2877–2890.
- Maughan, B.C., 2001. The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community. *J. Exp. Mar. Biol. Ecol.* 256, 59–71.
- McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of Ecological Communities, Chapter 9 Data Transformations. MjM Software Design, Glenden Beach, OR.
- Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250, 257–289.
- Murphy, M., Iken, K., 2014. Larval brachyuran crab timing and distribution in relation to water properties and flow in a high-latitude estuary. *Estuar. Coasts* 37, 177–190.
- Nasrolahi, A., Pansch, C., Lenz, M., Wahl, M., 2013. Temperature and salinity interactively impact early juvenile development: a bottleneck in barnacle ontogeny. *Mar. Biol.* 160, 1109–1117.
- Neal, E.G., Hood, E., Smikrud, K., 2010. Contribution of glacier runoff to freshwater discharge into the Gulf of Alaska. *Geophys. Res. Lett.* 37, L06404.
- Nielsen, M.M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P.B., Bruhn, A., 2014. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Mar. Biol.* 161, 2011–2022.
- Okamoto, D.K., Stekol, M.S., Eckert, G.L., 2013. Coexistence despite recruitment inhibition of kelps by subtidal algal crusts. *Mar. Ecol. Prog. Ser.* 493, 103–112.
- Opazo, L.F., Otaiza, R.D., 2007. Vertical distribution of spores of blade-forming *Sarcotelia crispata* (Gigartinales) and crustose corallines (Corallinales) in the water column. *Bot. Mar.* 50, 97–105.
- Perkol-Finkel, S., Airoldi, L., 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS One* 5, e10791.
- Pratt, D.R., Lohrer, A.M., Pilditch, C.A., Thrush, S.F., 2014. Changes in ecosystem function across sedimentary gradients in estuaries. *Ecosystems* 17, 182–194.
- Qiu, J., Qian, P., 1999. Tolerance of the barnacle *Balanus amphitrite amphitrite* to salinity and temperature stress: effects of previous experience. *Mar. Ecol. Prog. Ser.* 188, 123–132.
- Roleda, M.Y., Dethleff, D., 2011. Storm-generated sediment deposition on rocky shores: simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Mar. Biol. Res.* 7, 213–223.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675.
- Schoch, G.C., Chenelot, H., 2004. The role of estuarine hydrodynamics in the distribution of kelp forests in Kachemak Bay, Alaska. *J. Coast. Res.* 45, 179–194.
- Spurkland, T., Iken, K., 2011. Kelp bed dynamics in estuarine environments in subarctic Alaska. *J. Coast. Res.* 27, 133–143.
- Svendsen, H., Beszczynska-Moller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Orbaek, J.B., Bischof, K., Papucci, C., Zajackowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J., Dallmann, W., 2002. The physical environment of Kongsfjorden-Krossfjorden, and Arctic fjord system in Svalbard. *Polar Res.* 21, 133–166.
- Svensson, J.R., Marshall, D.J., 2015. Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. *Ecology* 96, 819–827.
- Valentine, J.P., Johnson, C.R., 2005. Persistence of sea urchin (*Heliocidaris erythrogramma*) barrens on the east coast of Tasmania: inhibition of macroalgal recovery in the absence of high densities of sea urchins. *Bot. Mar.* 48, 106–115.
- van Tamelen, P., Woodby, D., 2001. *Macrocystis* biomass, quality, and harvesting effects in relation to the herring spawn-on-kelp fishery in Alaska. *Alaska Fish. Res. Bull.* 8, 118–131.
- Vásquez, J.A., Piaget, N., Vega, J.M.A., 2012. The *Lessonia nigrescens* fishery in northern Chile: "how you harvest is more important than how much you harvest". *J. Appl. Phycol.* 24, 417–426.
- Walker, J.W., 2007. Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. *Mar. Ecol. Prog. Ser.* 331, 109–118.
- Wiencke, C., Clayton, M.N., Gomez, I., Iken, K., Luder, U.H., Amsler, C.D., Karsten, U., Hanelt, D., Bischof, K., Dunton, K., 2007. Life strategy, ecophysiology and ecology of seaweeds in polar waters. *Rev. Environ. Sci. Biotechnol.* <http://dx.doi.org/10.1007/s11157-006-0001-4>.
- Włodarsk-Kowalczyk, M., Weslawski, J.M., 2001. Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays. *Clim. Res.* 18, 127–132.
- Yorke, C.E., Miller, R.J., Page, H.M., Reed, D.C., 2013. Importance of kelp detritus as a component of suspended particulate organic matter in giant kelp *Macrocystis pyrifera* forests. *Mar. Ecol. Prog. Ser.* 493, 113–125.
- Zacher, K., Bernard, M., Bartsch, I., Wiencke, C., 2016. Survival of early life history stages of Arctic kelps (Kongsfjorden, Svalbard) under multifactorial global change scenarios. *Polar Biol.* 39, 2009–2020.